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Mechanical injury and occlusion: An urban, tropical perspective

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ABSTRACT

Eight common tree species used for urban landscaping were examined in this study for the effect of branch pruning on the rate and extent of wound closure (occlusion) and internal discolouration in the stem. Rate of wound closure when branches were removed with stem or branch of origin (flush cut pruning) and cuts made away from the branch collar (natural target pruning) were compared on all species over a 3-year period. Understanding the effects of pruning will benefit urban foresters in tree selection and potentially prevent downstream challenges associated with mechanical injury. The findings for all eight species supported the recommended guidelines of retaining the branch collar during pruning which has shown to facilitate effective wound closure. The exposed wood diameter (exposed) for all species were significantly reduced after the second growing season for injuries derived through natural target pruning but for the same period, injuries derived through flush cut pruning, only six species showed significant reductions in exposed wood diameter. Two other species (*Mimusops elengi* and *Lagerstroemia speciosa*) were observed to have no further reduction in exposed wood following the first growing season. Both wound inducing techniques (flush cut pruning and natural target pruning) resulted in no significant change in healing tissue production following the second growing season. Correlation analysis showed a strong positive relationship ($r = 0.8–0.9$) between the width of the wound and the length of discolouration in the stem, suggesting that smaller cuts were better suited to avoid extensive wound induced discolouration. This finding was further reinforced through visual observations of numerous pruning wounds of all eight species which showed that smaller cuts were better able to close over as opposed to larger wounds.

Introduction

Foresters have been pruning forest trees for centuries because pruning has the potential to enhance wood quality (O'Hara, 2007). Objectives of pruning can however, vary extensively – for example, wood quality enhancement in forest pruning is achieved through the pruning/thinning of crowded trees. Pruning of urban trees unlike forest trees is undertaken for safety over and beyond all other considerations. The presence of trees alongside infrastructures (e.g. buildings, footpaths or roadways) necessitates regular pruning because the result of a fallen branch or a fallen tree can have serious impacts on human life. Despite the different objectives, the concept and techniques of pruning in an urban and rural environment as well as the process of healing are exactly the same. However, after centuries of experience and extensive reports on various aspects of pruning (O'Hara, 1989; Nicolescu, 1999), there are still conflicting recommendations over a seemingly simple yet central concept.

To date, the general guidelines for urban pruning has been a technique commonly known as "natural target pruning" (Shigo, 1984b, 1985b; Neely, 1988a; O'Hara, 2007). This technique retains the branch collar on the primary stem while removing the rest of the branch hence the wood and callus that forms after pruning is likely to be free of defects and will possess greater wood strength (Guariguata and Gilbert, 1996). Following mechanical injury (e.g. pruning), the wood reacts both internally and at the surface. Shigo and Marx (1977) have described the internal reactions of wood as the compartmentalization of decay in trees (CODIT). This hypothesis is a process whereby branch wound occlusion (a process where trees form callus and clearwood over wounds) commences with the formation of callus over the branch wound. Callus typically originates from differentiation of parenchyma cells associated with the phloem and xylem (Pallardy, 2008) which start off as non-distinct cells. Similar to the techniques of pruning, there has been conflicting conclusions on the extent of occlusion. The process varies depending on species and on the size of the pruning wounds. The traditional method of pruning branches was to make a flush cut with the tree trunk but this method in recent times has been avoided as it has been shown to encourage the invasion of decay organisms into the main trunk (Shigo, 1984a,b; Haavik and Stephen, 2011). Therefore, the current recommendation encourages that branches should be removed outside the collar (woody attachment that connects a branch to the parent branch or trunk) – this technique facilitates a circular closure around the wound while flush

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cuts often result in a distorted closure that exposes the wood to discolouration and decay.

Additionally, the effects of season on the rate of wound closure have received considerable attention (Hudler, 1984; Shigo, 1984a; Perry and Hickman, 1987; Eyles et al., 2003; Fierke, 2008; Haavik and Stephen, 2011). Previous reports have shown that in temperate regions (Hudler, 1984; Shigo, 1984b; Perry and Hickman, 1987), pruning wounds made during the winter months tend to exhibit slower occlusion as compared to wounds made in spring. Though extensive data has been collected for rates of occlusion across seasons and amongst various species in the temperate regions, they cannot be applied to trees in the tropics as growth and occlusion in tropical regions can occur all year round. In contrast to the extensive research conducted for trees in temperate regions, much less is known about rates of occlusion in the tropics. Earlier reports (Harris, 1983; Shigo, 1984b; Perry and Hickman, 1987) have suggested that tree wound size, rate of occlusion, species of tree and vigor are important, in preventing wood decay and potential infection. Whilst recent reports (Fierke, 2008; Pallardy, 2008; Smith, 2008) suggest that wound width is directly proportional to the potential for decay and rate of closure (by callus tissue) – suggesting therefore, that a smaller wound would be less susceptible to wood decay as compared to a larger one that may take several years to close or will never completely close.

Though the concept and techniques of pruning are well founded with extensive research conducted on this subject, the effects of pruning on tropical, urban trees are less well documented in the literature – with only a handful of examples. One is a report on the variation in rates of trunk wound closure achieved through drilling conducted in the Panamanian lowland forest (Guariguata and Gilbert, 1996) and another, a study on sugar maple involving calcium manipulation (Huggett et al., 2007). Reports on wound closure in an urban environment are even scarcer. Furthermore, regular pruning is absolutely necessary in an urban landscape to keep the sites safe but, the associated effects of pruning (e.g. wood decay, wood discolouration and pathogenic invasion) can have a detrimental effect on the growth and safety of human activity that revolve around the landscape. Therefore, the identification of a species that possesses the potential to resist some of the damages associated with pruning will find a large and ready market in urban and municipal forestry programs. Therefore, this study was set up to (1) determine if the method of pruning has an impact on the rate and extent of occlusion in tropical urban tree species; (2) identify if the size of wound will affect the rate and extent of occlusion; (3) determine the consequences of wounding through the subsequent development of wound induced discolouration in stems and (4) identify the variability between species in rate and extent of occlusion.

Materials and methods

Site and species information

The experiment was conducted from 2009 through to 2012 involving eight species: *Peltophorum pterocarpum* (DC.) Backer ex K. Heyne, *Samanea saman* (Jacq.) Merr., *Pterocarpus indicus* Willd., *Khaya senegalensis* (Desr.) A. Juss., *M. elengi* L., *E. grandis* Wight., *Lagerstroemia speciosa* (L.) Pers. and *Milletia pinnata* (L.). The trees were grown by the side of the road exposed to natural conditions. The study was conducted in the northern end of the island of Singapore (Latitude 1.5° N and Longitude 104° E) with natural light with a mean daily photosynthetic photon flux density (PPFD) of 1300 μmol m^{-2} s^{-1}. The experimental species were positioned randomly comprising of five trees (with ten pruning wounds) per species in a complete randomized design. The experimental trees were between the ages of 5–8 years. The stem circumference (measured 1.3 m from the ground), height and crown size of the experimental trees are detailed in Table 1.

The experimental trees were grown in loamy clay soil consisting of 15–20% sand, 20–30% loam, and 25–40% clay using similar methods to those in Puckett et al. (1985). Organic matter present in the soil was between the ranges of 5–10% following the procedures of Schulte (1995). Apart from water received via rainfall, no other methods of irrigation were used.

Tree wounding

The wounds inflicted on the stems were at approximately the same height on the trees and within 2–5 m from the ground – the selection of trees and branches were based upon those that exhibited healthy growth trends. The size of wounds was between the ranges of 10–23 cm (width measurements). The wounds made were ellipses with rounded edges. Chisels were used to remove the bark and fully expose the wood.

Two pruning methods were applied to inflict wounds on the stem. The first method was a flush cut which is a technique of pruning the stem, branch or major limb back to the base. This involved cutting the stem or branch back against the trunk or parent limb (Fig. 1). The other method used is known as natural target pruning. This practice makes use of the branch collar to identify the appropriate location for branch removal. A three-cut process was used in this technique so as to ensure preservation of bark tissue and branch collar (Fig. 1) (Harris et al., 2003). Each experimental tree used in this study was exposed to wounds inflicted via both pruning methods.

Fig. 2.

Wound occlusion and cross sectional discolouration

Closure of wounds was determined on a monthly basis. Horizontal and vertical measurements based upon the greatest width and length of wood remaining exposed immediately following pruning was observed and the same readings were made once every month. The closure of wounds was generally divided into three categories: full closure, intermediate coverage and poor coverage (Fig. 3). For the measurement of wound induced discolouration in wood, branches were dissected and the extent of discolouration was established at their maximal extension points in an axial and tangential direction following the protocol used by Vasiliauskas (1998). Ninety-five branches each from two of the most common tree species (*S. saman* and *K. senegalensis*) used extensively in roadside tree planting in Singapore were observed. The maximal width and length of discolouration present over the branch cross section was measured. Since natural target pruning is set as the recommended guideline for urban tree pruning, the observation of stem discolouration was focused primarily on wounds inflicted by this method.

Statistical analysis

Data collected were subjected to an analysis of variance (ANOVA) and where appropriate, mean separation was performed using least significant difference tests (PROC ANOVA; SAS Institute, software Version 9, Cary, NC, USA). Treatment means were compared by least significant difference to determine whether means were significantly different at $P = 0.05$. Linear correlation analysis (Systat Software Inc., Sigma Plot 12, San Jose, CA, USA) was used to determine the relationship of cross sectional discolouration with that of wound width.

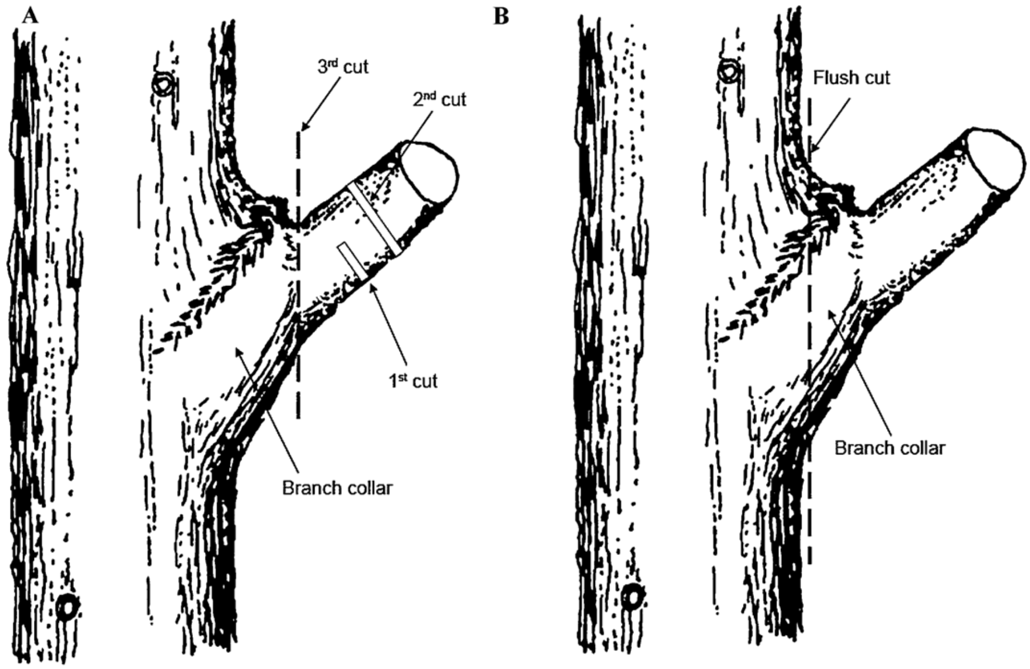

Fig. 1. Schematic illustration of the process of (A) natural target pruning and (B) flush cut pruning (Illustrations adapted from Modern Arboriculture–touch trees by Shigo, 1991).

Results

Tree growth

Tree growth performance for the eight species in this study was monitored monthly over a 3 year period. Mean annual circumference measurements indicated no significant change in the first two years following wounding (Table 1). Significant increments were only observed in the third growing season but for six out of the eight species (*S. saman*, *K. senegalensis*, *P. pterocarpum, P. indicus*, *E. grandis* and *M. pinnata*) examined in this study. Height measurements indicated that the same six species also showed a significant increase in height but this observation was made only within the first two years following wounding (Table 1). Four of these species (*S. saman*, *K. senegalensis*, *P. pterocarpum* and *P. indicus*) also showed a significant increase in crown area within the first two years but thereafter exhibited no significant change in the third growing season (Table 1). *M. pinnata* on the other hand, exhibited significant increments in crown area all throughout the study (Table 1).

Exposed wood width

The species studied differed in their ability to bring about wound closure. Observations made after the first and second year (following wounding), showed that exposed wood diameter were significantly different among all species for injuries inflicted through natural target pruning (Table 2). Conversely, for injuries inflicted through flush cut pruning, three species (*P. indicus*, *E. grandis* and *M. pinnata*) showed no significant change in exposed wood diameter, but five other species exhibited significant reductions in exposed wood diameter (*S. saman*, *K. senegalensis*, *P. pterocarpum*, *M. elengi* and *L. speciosa)* within the first year (Table 2). Observations made in the second year for injuries inflicted through flush cut pruning varied from those made in the previous year whereby six species (*S. saman*, *K. senegalensis*, *P. pterocarpum*, *P. indicus*, *E. grandis* and *M. pinnata*) had continued to significantly reduce exposed wood diameter whilst two other species (*M. elengi* and *L. speciosa*) which had in the first year exhibited a significant reduction in wood diameter, did not continue to bring about significant wound closure in the next growing season (Table 2).

Three years on, the method of flush cut pruning resulted in wounds that did not completely close but where injuries were inflicted through natural target pruning, for most species (*S. saman*, *K. senegalensis*, *P. pterocarpum*, *P. indicus*, *E. grandis* and *M. pinnata*), the rate of wounds that healed over fully, ranged between 40% and 100% (Table 2). The two exceptions were *M. elengi* and *L. speciosa* where only 20% of the wounds that were inflicted, healed over successfully (Table 2). Observations made on exposed wood diameter in the third growing season showed no significant change in exposed wood width for all species regardless of the pruning method employed (Table 2).

Branch/stem discolouration

Regression analysis for two of the most common tree species used in roadside tree planting is shown in Fig. 4. Wound width and length of wound induced discolouration exhibited the strongest positive relationship (Fig. 4). Visual analysis of pruning wounds regardless of pruning method indicated that the smaller wounds tended to close over with callus tissue more effectively than larger wounds (data not shown). A weak relationship between wound closure and stem circumference was observed. Synthesizing the data from Tables 1 and 2 with correlation analyses, it was observed that the relationship between growth and wound closure were relatively insignificant ranging between 0.13 to 0.2, 0.003 to 0.6 and 0.001 to 0.5 (data not shown) for stem circumference, height and crown area, respectively. These findings are suggestive that the rate of growth of each individual species does not appear to be the key factor controlling wound occlusion in the trees examined here.

Discussion

Development of pruning techniques

Following the work on compartmentalization (Shigo and Marx, 1977; Shigo, 1984a, 1985a), Shigo (in the mid-1980s) developed

Table 1
Growth parameters of 8 urban tree species over a 3-year period.

Tree species	Original circumference at BH (cm)	Circumference at BH after 2nd year (cm)	Circumference at BH after 3rd year (cm)	Original height (m)	Height after 2nd year (m)	Height after 3rd year (m)	Original projected crown area (cm^2)	Projected crown area after 2nd year (cm^2)	Projected crown area after 3rd year (cm^2)
Peltophorum pterocarpum	65.3 (0.09) ^{a}	68.6 (0.03) ^{a}	72.4 (0.06)^b	7.0 (0.008)^a	7.8 (0.003)^b	8.2 (0.01)^b	25.22 (0.002)^a	32.21 (0.01)^b	35.74 (0.009)^b
Samanea saman	82.5 (0.005)^a	85.1 (0.01) ^{a}	90.2 (0.003)^b	8.1 (0.003)^a	8.9 (0.007)^b	9.3 (0.005)^b	38.76 (0.01)^a	43.00 (0.008)^b	46.12 (0.02)^b
Pterocarpus indicus	78.2 (0.008)^a	80.9 (0.02)^a	85.4 (0.01)^b	7.5 (0.01)^a	8.0 (0.004)^b	8.1 (0.003)^b	32.93 (0.03)^a	38.87 (0.01)^b	40.98 (0.007)^b
Khaya senegalensis	84.5 (0.04)^a	86.0 (0.007)^a	91.1 (0.004)^b	8.3 (0.008)^a	9.1 (0.01)^b	9.5 (0.007)^b	41.75 (0.005)^a	46.56 (0.04)^b	48.20 (0.02)^b
Mimusops elengi	51.6 (0.009)^a	52.9 (0.03)^a	55.1 (0.01)^a	4.3 (0.01)^a	4.6 (0.006)^a	5.5 (0.006)^b	12.85 (0.01)^a	15.22 (0.008)^a	17.61 (0.006)^a
Eugenia grandis	62.4 (0.05)^a	65.9 (0.008)^a	71.1 (0.006)^b	6.9 (0.004)^a	7.6 (0.01)^b	8.1 (0.007)^b	29.67 (0.007)^a	31.93 (0.01)^a	38.89 (0.004)^b
Lagerstroemia speciosa	45.8 (0.04)^a	48.9 (0.002)^a	51.2 (0.04)^a	4.7 (0.005)^a	5.3 (0.02)^a	6.2 (0.01)^b	13.32 (0.01)^a	16.08 (0.004)^a	19.25 (0.01)^a
Milletia pinnata	53.5 (0.007)^a	55.7 (0.01)^a	61.0 (0.008)^b	7.1 (0.008)^a	8.2 (0.01)^b	8.5 (0.007)^b	26.43 (0.005)^a	32.78 (0.01)^b	39.57 (0.006)^c

BH stands for breast height. Values are means ± s.e. (in parentheses) $n = 5$; Different letters indicate means are significantly different at $P < 0.05$.

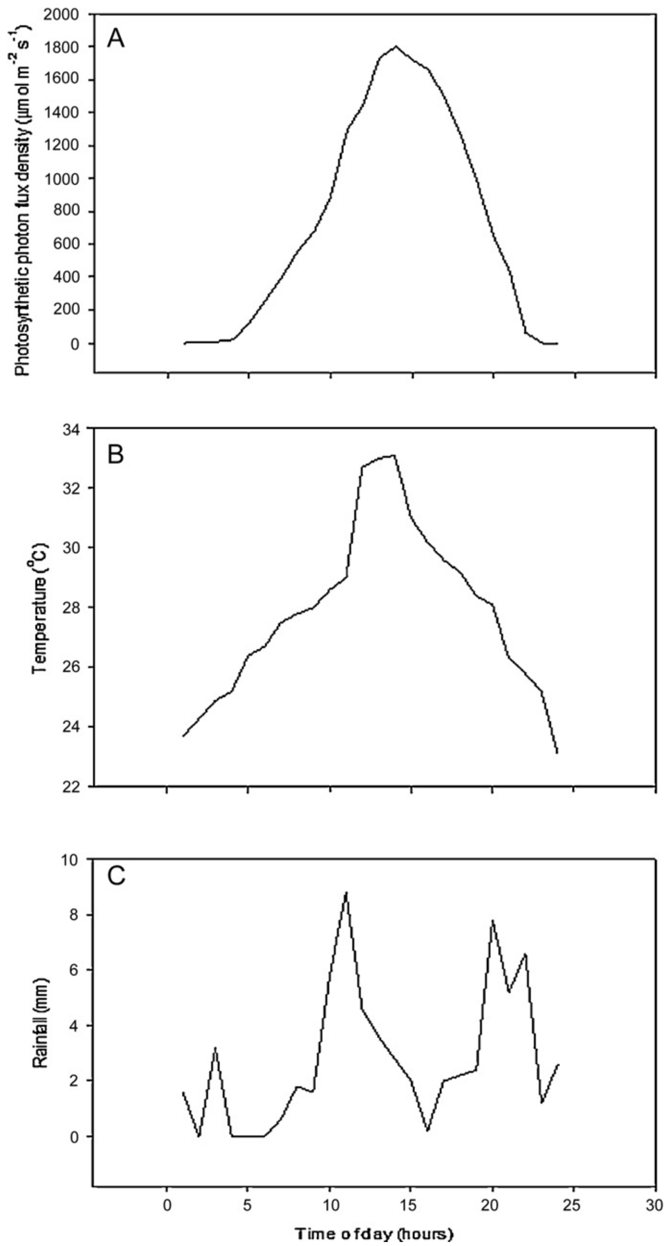

Fig. 2. Diurnal changes in environmental parameters on a typical sunny day at the experimental site (a) photosynthetic photon flux density (PPFD), (b) air temperature and (c) rainfall data (on a typical wet day).

the technique of "natural target pruning" that removes branches by cutting outside the branch collar (Fig. 1). This technique is in stark contrast to the earlier recommendation of flush cut pruning (Fig. 1) (Shigo, 1984b, 1985b; Neely, 1988a,b) which involves the removal of the branch collar and cutting flush with the tree trunk. Through his extensive work on tree pruning and occlusion, Shigo (1984b) concluded that the method of cutting flush with the tree trunk will usually lead to a myriad of defects, ranging from radial cracks, circumferential cracks, discolored wood and wood decay. Therefore, the recommendation was altered to retain the branch collar during the process of branch removal to serve as a protection zone as the remaining parts of the branch start to die away (Shigo, 1985b). This recommendation is supported by previous as well as recent reports (Green et al., 1981; Glass and McKenzie, 1989; Shigo, 1991; MacClaren, 1993; Brown, 2004; O'Hara, 2007), which have shown that the removal of the branch collar will leave the wound susceptible to internal spread of discolouration and decay. The primary

Fig. 3. Extent of callus formation over pruning wounds – illustrations show (A) good coverage of healing tissue for *Khaya senegalensis* (fully closed wound), (B) intermediate coverage of healing tissue for *Samanea saman* and *Peltophorum pterocarpum* and (C) poor coverage of healing tissue for *Mimusops elengi* and *Lagerstroemia speciosa*.

goal of retaining the branch collar was to meet the sole objective of maintaining tree health, giving the tree the best chance to occlude efficiently and prevent infection as the collar contains a chemical zone which inhibits the spread of decay in the trunk (Pearce, 2000; Rajput and Rao, 2007).

Pruning wound and occlusion

The process of occlusion is important because it facilitates the covering of the wound with bark and new wood (O'Hara, 2007) – efficient occlusion is a key defence against infection by stem decay fungi (Shigo, 1986). It is noteworthy however, that wound healing is more than just wound closure or callus formation. There are at least two internal defence mechanisms that serve as chemical barriers that keep out wood-destroying microorganisms and the other system that is in place serves to wall off or confine the infected area. Extensive research has been conducted on this subject (Mayer-Wegelin, 1936; McQuilkin, 1950; Boyce, 1961; Biggs, 1992; O'Hara and Buckland, 1996; O'Hara, 2007). In fact, there have been studies conducted since the early 20th century (Des Cars, 1900; Davey,

Table 2
Effect of pruning technique(s) on the rate and extent of occlusion in 8 urban tree species.

Tree species	Pruning technique	Original wound width (cm)	Width of wood exposed after 1st year (cm)	Width of wood exposed after 2nd year (cm)	Width of wood exposed after 3rd year (cm)	Number of wounds fully closed after 3 years (of 10 wounds)
Peltophorum pterocarpum	F	15.3 (0.002)^{c}	10.4 (0.07)^{b}	7.5 (0.003)^{a}	7.0 (0.01)^{a}	0
	NT	15.0 (0.004)^{c}	9.2 (0.009)^{b}	5.8 (0.01)^{a}	4.8 (0.004)^{a}	2
Samanea saman	F	21.4 (0.02)^{c}	16.7 (0.006)^{b}	12.3 (0.007)^{a}	10.8 (0.02)^{a}	0
	NT	21.8 (0.007)^{c}	13.2 (0.005)^{b}	9.5 (0.01)^{a}	7.2 (0.008)^{a}	3
Pterocarpus indicus	F	22.1 (0.009)^{b}	20.9 (0.01)^{b}	16.7 (0.006)^{a}	15.1 (0.02)^{a}	0
	NT	22.9 (0.01)^{c}	18.3 (0.005)^{b}	13.4 (0.01)^{a}	11.5 (0.007)^{a}	3
Khaya senegalensis	F	20.7 (0.005)^{c}	13.3 (0.02)^{b}	7.8 (0.008)^{a}	7.1 (0.006)^{a}	0
	NT	20.2 (0.04)^{c}	10.5 (0.005)^{b}	3.0(0.01)^{a}	NA	5
Mimusops elengi	F	11.6 (0.01)^{b}	8.9 (0.005)^{a}	7.8 (0.01)^{a}	6.4 (0.007)^{a}	0
	NT	12.0 (0.03)^{c}	7.2 (0.008)^{b}	5.9 (0.03)^{a}	5.7 (0.01)^{a}	1
Eugenia grandis	F	16.6 (0.006)^{b}	15.3 (0.01)^{b}	10.4 (0.008)^{a}	10.0 (0.03)^{a}	0
	NT	17.0 (0.008)^{c}	10.7 (0.04)^{b}	7.7 (0.01)^{a}	7.3 (0.009)^{a}	3
Lagerstroemia speciosa	F	11.0 (0.01)^{b}	7.5 (0.006)^{a}	6.2 (0.02)^{a}	5.8 (0.009)^{a}	0
	NT	10.7 (0.01)^{c}	6.1 (0.03)^{b}	4.1 (0.01)^{a}	4.9 (0.007)^{a}	1
Milletia pinnata	F	15.2 (0.04)^{b}	13.5 (0.005)^{b}	9.8 (0.009)^{a}	8.9 (0.02)^{a}	0
	NT	15.5 (0.009)^{c}	9.3 (0.01)^{b}	5.7 (0.01)^{a}	5.0 (0.007)^{a}	4

F stands for flush cuts. NT stands for natural target pruning. Values are means ± s.e. (in parentheses) $n = 5$ [5 experimental trees per species. Each tree with 2 wounds (F and NT)]; Different letters indicate means are significantly different at $P < 0.05$.

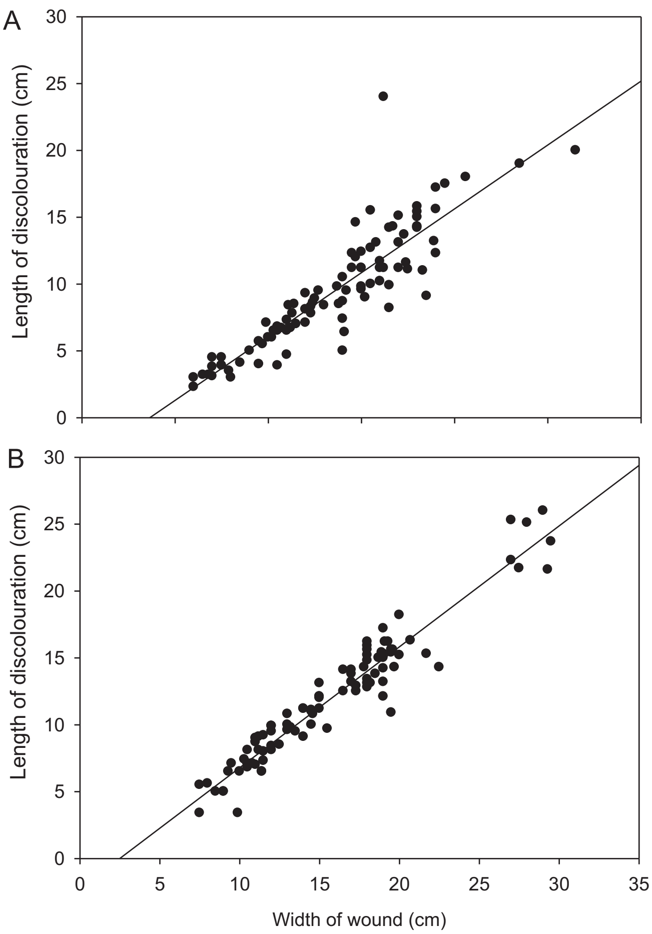

Fig. 4. Relationships between the extent of lateral spread of discolouration as a function of the width of wound for (A) *Khaya senegalensis* and (B) *Samanea saman* – the relationships have the following regression equations (A) $y = 0.9553x - 3.4751$ ($R^2 = 0.78$) and (B) $y = 0.904x - 2.2456$ ($R^2 = .93$).

1907; Webster, 1916; Peets, 1925; Brooks and Moore, 1926; Cline and Fletcher, 1928; Curtis, 1936, 1937). The methods of pruning are well documented in the literature but most reports have been carried out predominantly in the temperate regions (Hudler, 1984; Shigo, 1984b, 1991; Perry and Hickman, 1987; Uotila, 1990; Bedker et al., 1995; Emmingham and Fitzgerald, 1995; Chiu et al., 2002; Muzika and Guyette, 2004; Brodie and Harringston, 2006) with little known about the species in the tropics and how occlusion will take place in the tropical region (Guariguata and Gilbert, 1996; Huggett et al., 2007; Rajput and Rao, 2007). The process of occlusion in the tropics can be quite variable given that growth occurs throughout the entire year. Moreover, even much less is known about occlusion in an urban environment where trees are exposed to harsh growing conditions (e.g. constrained planting spaces and polluted atmospheric conditions). Furthermore, regular pruning is necessary in an urban environment given that safety (e.g. branch shedding) and foliar obstructions can have serious impacts on human activity. These reasons substantiates the need for more research focusing on pruning and wound occlusion in tropical tree species and especially on trees growing in an urban environment.

The findings for eight urban, tropical tree species collectively indicate that the method of flush cut pruning is not beneficial to wound occlusion (Table 2). Conversely, the technique of natural target pruning has been shown to be the better of the two as the percentage of fully closed wounds rose from 0% to between 40 and 80% (Table 2). This finding is consistent with that of previous reports (Green et al., 1981; Neely, 1988a,b; Glass and McKenzie, 1989; Shigo, 1991; MacClaren, 1993; Brown, 2004; O'Hara, 2007). Interestingly, the ability to heal over effectively may be species specific – whereby some species exhibit fully closed wounds whilst others are only capable of an intermediate coverage. For example, all 5 wounds inflicted on *K. senegalensis* via the method of natural target pruning had fully callused over within 2 years. This observation was unique to this species only. This suggests that the fundamentals to the extent of healing tissue production and coverage may be genetic in nature but the underlying mechanisms are beyond the scope of this research. It does however, warrant future research into the underlying mechanisms of pruning and wound occlusion in tropical, urban trees.

Of the eight species studied, *Mimusops elenegi* and *L. speciosa* had the lowest rate of fully closed wounds (after 3 years) and this included the wounds inflicted via the method of natural target pruning which was considered the better of the two techniques (Table 2). A plausible explanation to this observation is the relatively slower rate of growth observed in both these species, particularly in radial stem growth (Table 1). Positive correlations between rates of wound closure and radial stem growth have been observed in previous reports involving temperate trees (Neely, 1983, 1988b; Guariguata and Gilbert, 1996). However, for the tropical trees examined here, the regression correlations for stem circumference and wound occlusion (data not shown) though positive, did not show a particularly strong relationship. Furthermore, it should be noted that our observations are limited to describing the external signs of wound closure only. The suite of chemical and anatomical changes that occur internally following stem wounding have been described for many temperate tree species (Shigo, 1984a) and it is possible that those responses may occur in tropical trees as well. Such mechanisms associated with wound occlusion are an area for future research on tropical urban trees.

Taken together, the variability in wound closure observed here can be attributed to the varying internal wound defense and healing responses employed by each species. Analysis of a wider range of species particularly of faster growing species in future studies should help clarify if efficient and effective wound responses are associated with growth strategies of trees (Hudler and Jensen, 2002).

The spread of discolouration after pruning

The results for the spread of wound induced discolouration in this present study indicate a strong positive relationship between wound width and the extent of discolouration in a pruned stem (Fig. 4). Similar relationships have been found with *Quercus robur*, *Alseis blackiana*, *Gustavia superb*, *Miconia argentea*, *Poulsenia*, *armata*, *Protium panamense*, *Protium tenuifolium* and *Tetragastris panamensis* (Guariguata and Gilbert, 1996; Vasiliauskas, 1998), supporting the conclusion that wounds of smaller widths are more likely to effectively isolate or contain the column of discolouration as oppose to wounds with greater diameters. Earlier reports by Neely (1988a,b) had however observed that the larger the wound, the more callus was produced and that healing was more efficient for larger as opposed to smaller wounds. The conflicting observations may be attributed to different species and the highly variable age of the trees observed in these studies.

Lastly, it should be emphasized that despite the efficient and effective response to wound occlusion observed in *K. senegalensis*, there was still discolouration within the pruned stems. This observation is suggestive that whilst the ability to effectively heal over with callus tissue is critical as a defense against infection by stem decay fungi, the rate (e.g. time, speed) of occlusion also plays an important role in internal stem decay and discolouration.

Conclusion

The study's findings suggest that there are striking differences in the ability for wound occlusion between species but the observations here also suggest that occlusion (if any) occurs within a 2-year period. *K. senegalensis* was identified as the better healer among the tree species examined in this study. The findings and conclusions derived from this study, develops further considerations for branch pruning in an urban environment. The main traits that is important to reducing susceptibility to wound induced discolouration lies in the correct pruning method, a less extensive pruning wound and species of tree. The correlation between growth and wound closure was far less significant. Future research should focus on the underlying defence and healing responses of tropical species in the urban environment as the findings here are suggestive that wound closure and isolation of infected tissue might have a genetic or cellular association. A holistic understanding will facilitate to clarify the differences in the rate and extent of occlusion across different species, such knowledge will benefit urban foresters in their process of tree selection and prevent potential downstream issues associated with mechanical injury.

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